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THE SPECIES OF *TAMANDUA* GRAY (EDENTATA, MYRMECOPHAGIDAE)

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Over an extensive range from southern México to northern Argentina and Uruguay, the anteaters of the genus *Tamandua* display great variation in colors of coats and in proportions of skulls. Central American populations are black-vested, but in South America the pelage varies from a monochromatic black, brown, tan or white through a gradient of bichromatic patterns to a black-vested condition. After a taxonomic history in which writers gave not less than ten specific names to the tamanduas, treatment of the genus during this century has been chiefly either (1) as containing two species—*T. tetradactyla* L. for the black-vested forms and *T. longicaudata* (Wagner) for those lacking a complete vest, or (2) as monotypic, the species *T. tetradactyla* containing different subspecies of which one was the nonvested or partially vested *T. t. longicaudata.* One melanistic form, *nigra* Geoffroy, has been assigned to either of the two species, while a second melanistic form, *quichua* Thomas, has been more uniformly retained as a subspecies of *T. tetradactyla.*

This study was initially concerned with the identification of the extensive series of *Tamandua* collected by the Smithsonian Venezuelan Project under the direction of Dr. Charles O. Handley, Jr. The black-vested tamanduas of northwestern Venezuela proved to be distinctly separable from the geographically adjoining samples of nonvested forms from a variety of habitats. In turn, the nonvested forms were bound through a clinal chain to black-vested forms south of Venezuela.

Correlating these two differences—a disjunction line in northwestern Venezuela and a cline to the south—with taxonomic levels required samples from areas well beyond the original focus of the study. To this end, I examined specimens which were available in other collections from throughout the range of the genus.

Procedures

Color and Color Patterns: I recorded patterns of pelage (Fig. 1) as:

A) Vested. A vivid black area on the trunk, continuous from black shoulder stripes posteriorly to the rump and widening behind the shoulders to encircle the body. This vest is surrounded by a uniformly pale color of white, tan or gold on the rest of the body, the legs, and the heavily furred base of the tail. The pale color also divides the vest as a middorsal stripe from the neck to the middle or posterior portions of the back. Such pelage is found in all specimens from the northwestern portion of the range of the genus (AMNH 17272, México, Vera Cruz, Pasa Nueva; USNM 443242, Venezuela, Zulia, El Rosario) and from the lower Amazon basin south to Uruguay (NRMS 508, Brazil, Pará, Cametá; Uruguay, Cerro Largo, Estancia La Formosa, see Ximénez, 1972: plate).

B) Nonvested. Specimens have completely uniform pelage, light tan, buffy white, or gold in color, with no obvious indication of vest pattern (USNM 441973, Venezuela, Falcón, Capatárida; ROM 31883, Guyana, Rupununi, Dadanawa Ranch). In some specimens (USNM 441971, Venezuela, Capatárida) a vague vest pattern could be seen only by parting the hairs, as the bases of hairs were slightly darker than the tips.

C) Partially Vested. Obvious appearances of the vest first occur usually in the shoulder area as smudges or even vivid stripes, though the rest of the body is uniformly pale (ANSP 4635, probably Chapada, Mato Grosso, Brazil, holotype of *M. bivitatta straminea* Cope). At the darker end of the gradient, the vest appears grizzled or gray because of dark hairs with tan tips; black shoulder stripes usually accompany this coloration (FMNH 25261, Bolivia, Santa Cruz; USNM 361029, Guyana, Dadanawa Ranch). In searching for correlations of variation in pelage with cranial and external measurements and proportions, I rated the gradient from completely pale and uniform pelage to the nearly complete pattern of the vest as stages of one to nine.

D) Melanistic. Specimens in this category have overall, completely black (BMNH 27.1.1.156, Perú, San Martín, Yurac Yacu, holotype of *M. t. quichua* Thomas) or dark brown pelage. Variants, not recorded as melanistic, are individuals with pale foreheads and legs but with uniformly dark brown pelage from ears to rump. This color form, as well as those with uniformly dark brown pelage, strongly suggests a gradient from complete melanism to the partially vested condition.

Variation in Pelage by Age, Sex, and Season: I found no major

FIG. 1. Localities of *Tamandua* specimens examined. Three peripheral records from the literature are added: I, Dalquest, 1953; II, Carvalho, 1962; III, Ximénez, 1972.

changes in pelage between immaturity and adulthood; but specimens of young tamanduas have longer dorsal hair, in proportion to size of the body, which gives them a fluffy appearance. In addition, the immature vested specimens tend to have a greater proportion of pale hairs visible in the vest areas. Aside from this I found no basis for statements by Azara (1801:107) and Liais (1872:360) that color variation is correlated with age. No pronounced sexual difference in pelage was found except that in localities presenting a gradient of partially vested forms, the darker specimens are usually males (USNM 406686, female, Capibara vs. USNM 406688, male, San Juan de Río Manapiare, both from Territorio Amazonas, Venezuela). One sample (Guyana, Dadanawa Ranch, in USNM and ROM) is large enough to demonstrate that there is little or no seasonal variation in pelage. However, more data are needed on this point and on rates of growth of hair and hair replacement.

Cranial Characters: Each skull was assigned to one of five arbitrary age classes on the basis of sequence of closure of sutures. Measurements of skulls in age classes 0 and 1 (no closures except for sutures of the occipital in class 1) were not included in geographical comparisons because of the magnitude of differences in proportions and measurements, particularly shorter and narrower rostra. Age class 1 was considered a stage of transition to sexual maturity as the Smithsonian Venezuelan Project collected a few females of this age with embryos. Comparison of adult males and females (age classes 2–5) from similar geographical areas revealed no significant sexual differences in cranial measurements or proportions.

The following cranial dimensions and their abbreviations are included in this paper (Fig. 2):

ARW—anterior rostral width; taken with the anterior flat face of the calipers at the level of the most posterior lateral indentation of the anterior part of the maxilla.

FMW—maximal width of foramen magnum.

IFL—infraorbital foramina, mean of minimal lengths of pair.

NL-a, NL-b—nasal bones: a, minimal length at midline and b, maximal length.

OL—occipito-nasal length, distance from maximal posterior extension of occipital, dorsal to the formen magnum, to anterior tip of nasal bone.

RL—rostral length, derived as in the altitude of a triangle where the distance between the lacrimal foramen to the anterior tip of the nasal bone (probably the RL of Reeve, 1942 and Davis, 1955) is considered the hypotenuse and half the antorbital width is considered the base.

PRL—post-rostral length, derived as the difference between OL and RL.

AOB—antorbital breadth, minimal width of skull at the level of the lacrimal foramina.

ORB—interorbital breadth, minimal width between the middorsal borders of the orbits.

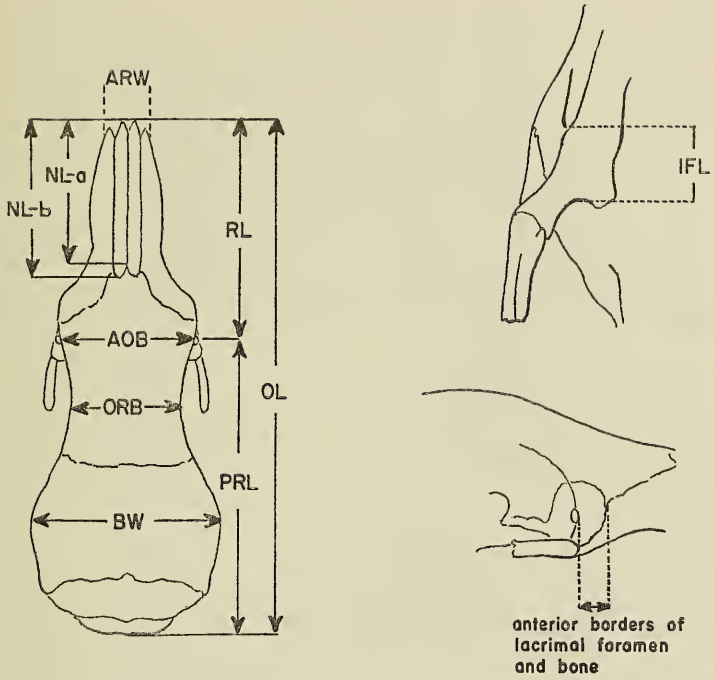

FIG. 2. Illustration of measurements of skulls of *Tamandua.*

BW—breadth of braincase, maximal breadth of skull posterior to zygomatic processes.

Two cranial characters that were scored, rather than measured, proved to have taxonomic value (Fig. 3):

1) The presence of four pairs of foramina (optic, orbital fissure, foramen rotundum, foramen ovale) in the orbit or only three pairs. The latter condition is caused by the absence of a bony septum between the orbital fissure (= anterior lacerate foramen) and the foramen rotundum. Bilateral asymmetry in some of the specimens required an averaging of this condition between left and right sides as well as partial scoring for incomplete septa. Since these septa are incompletely ossified in the youngest specimens, as well as more easily destroyed in the cleaning of immature skulls, no count of septa for immature specimens is included in the geographical comparisons.

2) The shape of the posterior (palatal) border of the infraorbital foramen. The maxilla either (a) extends as far, or farther, posteriorly on the medial side of the foramen as it does on the lateral side, resulting

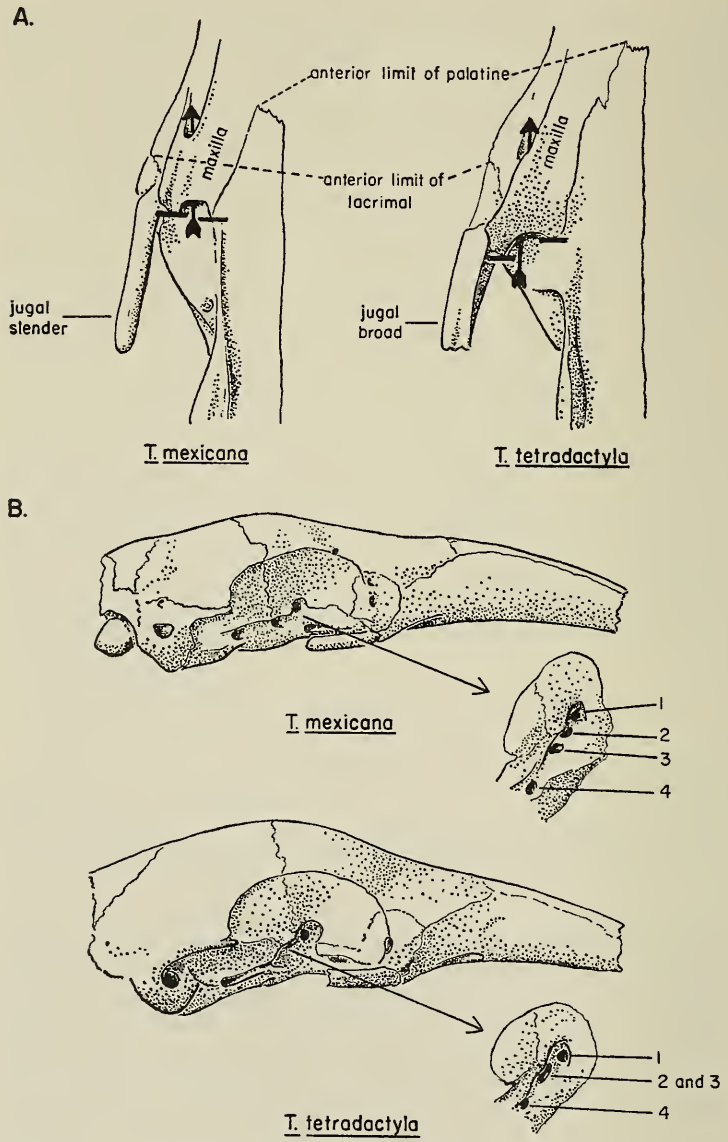

Fig. 3. Comparison of selected cranial characters in *Tamandua. T. mexicana*, CONN 16875, Chepo, Panamá; *T. tetradactyla*, CONN 16831, Km 285, Trans-Chaco highway, Paraguay. Both are black-vested specimens.

in a crescent-shaped border of the foramen, or (b) terminates on the medial side of the foramen distinctly anteriorly to the lateral side, resulting in a subequal or incomplete crescent-shaped border of the foramen.

When compared with the distances between the anterior border of the lacrimal foramen and bone (Fig. 2), the distances between the anterior borders of the palatine and lacrimal bones (parallel to the long axis of the skull, Fig. 3) are proportionally different between the two species.

Count of Vertebral Regions: A total of 39 vertebral columns was examined, but only individual vertebral regions that were without missing vertebrae are included in the diagnoses of the species. My count of the sacral region began with the first vertebra completely articulating with the ilia and ended with the last vertebra completely articulating with the ischia.

Sources of Specimens: Although tamanduas from over 40 collections have been examined, only the following collections and their curators at the time of study are cited here: AMNH—American Museum of Natural History, New York; Richard G. Van Gelder. ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia; H. Radcliffe Roberts. BMNH—British Museum (Natural History), London; G. B. Corbet. CONN—University of Connecticut Museum of Natural History, Storrs; Robert E. Dubos. FMNH—Field Museum of Natural History, Chicago; Joseph Curtis Moore. MCZ—Museum of Comparative Zoology, Harvard University, Cambridge; Barbara Lawrence. MNHN—Muséum National d'Histoire Naturelle, Paris; F. de Beaufort and Jean Dorst. MZUV—Musée Zoologique de l'Université et de la Ville, Strasbourg; F. Gouin and Jean-Pierre Rieb. NRMS—Naturhistoriska Riksmuseet, Stockholm; Ulf Bergström (deceased) and Greta Vestergren. PARA—Museu Paraense "Emílio Goeldi," Belém; Fernando C. Novaes. ROM—Royal Ontario Museum, Toronto; Randolph L. Peterson. SMF—Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main; Heinz Felten. TCWC—Texas Cooperative Wildlife Collection, Texas A & M University, College Station; Dilford C. Carter. USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Charles O.

←

A. Views of right palate. Infraorbital foramen is marked by an arrow and the medial and lateral margins of the posterior opening, by bars. Compare: posterior limits of maxilla on either side of foramen, anterior limits of the palatine and lacrimal bones, and dimensions of jugal bone.

B. Right side of skulls and detailed view of orbits, tilted to show foramina. 1, optic foramen; 2, orbital fissure; 3, foramen rotundum; 4, foramen ovale. Foramina 2 and 3 are separate in *T. mexicana* but combined in *T. tetradactyla* or separated by a deeply set, slender septum which is visible from lateral view only at its base.

Handley, Jr. ZSM—Zoologische Sammlung des Bayerischen Staates, Munich; Theodor Haltenorth.

Genus *Tamandua* Gray

Tamandua Gray, 1825:343.
Tamanduas F. Cuvier, 1829:501.
Uroleptes Wagler, 1830:36; Palmer, 1899:73.
Dryoryx Gloger, [1841]:112.

The black-vested populations of *Tamandua* are separated by 2,000–3,000 kilometers (1,200–2,000 miles) containing the intervening nonvested, partially vested, and melanistic forms (Fig. 1). The vested group occupying the northwestern part of the range of the genus (México to northwestern Venezuela) has been traditionally placed in the same species, *T. tetradactyla*, with the vested group in the southeastern portion of the generic range (Amazon basin to southeastern Brazil and northern Argentina). The few comparisons that have been made over much of the range of the genus, such as Allen (1904), Krumbiegel (1940), and Reeve (1942), have assumed a specific relationship of these two vested populations. Krumbiegel and Reeve, as well as Schröder (1937), then considered the question of the uniqueness of the nonvested and partially vested forms. Upon finding these *T. longicaudata* clinally integrating with *T. tetradactyla* in Brazil, and lacking specimens for adequate comparison of the two forms at their juncture in Venezuela, these writers concluded that *Tamandua* was a monotypic genus.

Because of the new material collected by the Smithsonian Venezuelan Project, as well as the opportunity to study many other specimens not seen by the previous authors, I could compare *longicaudata* at all of its boundaries with the vested tamanduas. Geographical gradients in both pelage and skulls were found between the southern populations of vested tamanduas and the *longicaudata* pelage forms. This was particularly evident in the Amazon basin where a gradual cline occurred from nonvested and partially vested *longicaudata* in eastern Ecuador, Perú, and western and central Brazil to vested *tetradactyla* in eastern Amazonas to eastern Pará, Brazil. A south-to-north gradient was found between the vested forms from the left or north bank of the Rio Amazonas to *longicaudata* of the Guyana highlands. To the north, the Río Orinoco proved to be only a partial barrier for *longicaudata*.

The second question was the taxonomic level of distinction between the black-vested tamanduas west of the Andes and those lacking complete vests and occurring immediately east of the Andes. This question involved comparing specimens from (a) either side of the Andes in Ecuador, (b) the Río Magdalena valley with those from the eastern side of the Cordillera Oriental in Colombia, and (c) northwestern Venezuela and Colombia with those from adjacent Venezuela and Colombia east of the Cordillera Oriental. All of these comparisons indicated

TABLE 1. Comparison of the species of *Tamandua*.

mexicana	*tetradactyla*
Black vest always present	Color of pelage geographically variable; black vest always present only in portions of range most distant from *T. mexicana*
Ear shorter (means 40–46 mm)	Ear longer (means 50–54 nearest to range of *T. mexicana*)
Skull slender (means of AOB, ORB, and BW less than 34, 25, and 42 mm)	Skull broad (means of AOB, ORB, and BW greater than 34.5, 25, and 41.5)
4 pairs of orbital foramina in most skulls	3 pairs of orbital foramina in most skulls
Posterior border of infraorbital foramen distinctly crescent shaped	Posterior border of infraorbital foramen an incomplete crescent; maxilla forming subequal borders about foramen
Jugal bone slender (height usually no more than 31% of length)	Jugal bone broad (height more than 31% of length)
Distance between anterior borders of palatine and lacrimal bones proportionally less	Distance between anterior borders of palatine and lacrimal bones proportionally greater
Caudal vertebrae 40–42	Caudal vertebrae 31–39

major lines of interruption coinciding with the Andean chain. This separation within the genus is abrupt, certainly not clinal as are the variations that extend from this point to the peripheries of the range, and is of such a major nature as to require consideration of two species: (1) a black-vested species, *T. mexicana*, occurring west of the eastern Andean divide from northwestern Venezuela and the Pacific slope of northern Perú to México, and (2) a black-vested to nonvested species confined to South America east of the Andes and including the nominate form, *T. tetradactyla*, as well as geographical color variants such as *longicaudata*, *quichua*, and *nigra*. The comparison of these two species is presented in Table 1. All measurements are in millimeters. The lists of synonyms, although incomplete, include most of the original names and new combinations, the names used in the more comprehensive studies of the genus, and the names used by the standard references for the two continents (Cabrera, 1958; and Hall and Kelson, 1959). Holotypes and certain other critical specimens that I have examined are cited.

Tamandua mexicana (Saussure)

Myrmecophaga tamandua (?), Desm. (var. *Mexicana*, Sauss.) Saussure, 1860:9.

Tamandua tetradactyla.—Tomes, 1861:287; Sclater, 1871:546.

Myrmecophaga tetradactyla.—Frantzius, 1869:307.

Tamandua bivittata Var. 3. *Opistholeuca* Gray, 1873a:27, only the specimens from Central America and Colombia. Lectotype (herewith selected): BMNH 50.7.8.39, skin and skull, "Colombia," coll. Parzudaki; labeled as "type"; listed by Gray as the second syntype.

? *Tamandua tetradactyla*, var. *leucopygia* Gray, 1873b:469. Colombia, Antioquia, Concordia or Medellín. Nomen nudum; although BMNH 73.4.23.8, same locality, coll. J. K. Salmon, was probably the basis for this name, Gray did not support his name with description, reference, or indication.

? *Myrmecophaga quadridactyla* True, 1884:588, in part. Nomen nudum.

Myrmecophaga sellata Cope, 1889:133. Type-locality: Honduras.

Tamandua tetradactyla instabilis Allen, 1904:392; Krumbiegel, 1940:174; Reeve, 1942:300; Cabrera, 1958:204. Holotype: AMNH 23420, Colombia, Magdalena, Bonda.

Tamandua tetradactyla tenuirostris Allen, 1904:394. Holotype: AMNH 17272, México, Vera Cruz, Pasa Nueva.

Tamandua tetradactyla chiriquensis Allen, 1904:395; Krumbiegel, 1940: 172; Hall and Kelson, 1959:238. Holotype: AMNH 18883, Panamá, Chiriquí, Boquerón.

Tamandua tetradactyla mexicana.—Allen, 1906:200; Reeve, 1942:300; Hall and Kelson, 1959:239.

Tamandua tetradactyla punensis Allen, 1916:83; Cabrera, 1958:204. Holotype: AMNH 36452, Ecuador, Isla Puná.

Tamandua tetradactyla sellata.—Goldman, 1920:63, footnote; Lönnberg, 1937:27; Krumbiegel, 1940:172.

Tamandua tetradactyla tambensis Lönnberg, 1937:25. Holotype: NRMS 18, Colombia, Cauca, El Tambo.

Tamandua tetradactyla tetradactyla.—Reeve, 1942:300, in part in which *T. t. chiriquensis, tambensis,* and *punensis* are considered as probable synonyms of subspecies *tetradactyla*.

Tamandua tetradactyla hesperia Davis, 1955:558; Hall and Kelson, 1959: 238. Holotype: TCWC 5322, México, Guerrero, near Acahuizotla.

Type-locality: México, Tabasco (Saussure, 1860:9).

Range: From the lower forested slopes of the southern edge of the Mexican plateau, in southeastern San Luis Potosí, Guerrero, and northwestern Oaxaca, through Central America to northwestern Venezuela, the valleys and montane forests of Colombia west of the divide of the Cordillera Oriental, and south in the forested coastal and Pacific Andean slopes of Colombia, Ecuador, and northwestern Perú (Fig. 1).

Diagnosis: *Pelage*—always black-vested on a paler background, rather

than uniformly black, brown or tan. *Ear*—range of means of length from notch, 40–46. *Skull*—slender, with means of AOB, ORB and BW for all samples falling below 34, 25 and 42, respectively, except for a gradient to larger skulls in the upper valleys of Río Cauca and Río Magdalena in Colombia; four orbital foramina (Fig. 3B) present in at least one side of all skulls from southeastern part of range of species and present in both sides of skulls of 80–100% of all specimens except for those from Guerrero, México (70%), and coastal Ecuador (60%); posterior (palatal aspect) border of infraorbital foramen (Fig. 3A) distinctly crescent-shaped and formed entirely by maxilla, with medial border of foramen extending as far posteriorly as (or farther than) lateral border; distance (measured perpendicular to midline of skull) between most anterior extension of palatine and lacrimal bones (Fig. 3A) less than half the distance between anterior borders of lacrimal foramen and lacrimal bone (Fig. 2); jugal (malar) slender (Fig. 3A), its greatest height usually 31% or less of its greatest length. *Vertebral count*—14 specimens from México (1, FMNH), Guatemala (3, USNM), Honduras (1, FMNH), Panamá (1, CONN), and northeastern Colombia (7, AMNH; 1, USNM): cervical 7 (in 10); thoracic 17.0 (15–18, in 11); lumbar 2.4 (2–3, in 14); sacral 5 (in 14); caudal 40.8 (40–42, in 8).

Comparison: See Table 1.

Tamandua tetradactyla (Linné)

Myrmecophaga tetradactyla Linné, 1758:35.

Myrmecophaga myosura Pallas, 1766:64. Type-locality: Brazil.

Myrmecophaga tamandua G. Cuvier, 1798:143. No locality; pelage described as "jaunatre."

Myrmecophaga nigra Geoffroy St.-Hilaire, 1803:217. "La Guyane?" In part: Azara, 1809:plate 7; Desmarest, 1817:107.

Myrmecophaga tamandua Geoffroy St.-Hilaire, 1803:217, in part [based upon both *M. tridactyla* L. and *T. tetradactyla* (L.)]. No locality.

Myrmecophaga bivittata Desmarest, 1817:107. Brazil.

Uroleptes tetradactyla.—Wagler, 1830:36.

Myrmecophaga tridactyla (not Linné, 1758:35).—McMurtrie, 1831:166, as synonym of *M. tamandua* Cuv.

Tamandua crispa Rüppell, 1842:179. "Guiana." Holotype not listed in Mertens, 1925, nor found in SMF in 1970.

Tamandua tetradactyla.—Gray, 1843:191. Brazil.

Myrmecophaga longicaudata Wagner, 1844:211. Type-locality restricted to Surinam by Cabrera, 1958:203.

? *Myrmecophaga longicaudata* Turner, 1851:218. No locality or reference, nomen nudum.

Uroleptes bivittatus.—Fitzinger, 1860:395. Brazil.

Tamandua bivittata.—Gray, 1865:384. Brazil, Paraguay.

Tamandua ursina.—Gray, 1865:384, as synonym for *T. bivittata*.

Tamandua longicaudata.—Gray, 1865:384; Allen, 1904:385.
Tamandua brasiliensis Liais, 1872:360. Brazil.
Tamandua bivattata. Var. 1. *Opisthomelas* Gray, 1873a:27. Lectotype (herewith selected): BMNH 40a, skin, Brazil, coll. Lt. Mawe; labeled as type; first in Gray's list of syntypes.
? *Myrmecophaga quadridactyla* True, 1884:588, in part. Nomen nudum.
Tamandua tamandua.—Jentink, 1888:215. Surinam.
Myrmecophaga bivattata straminea Cope, 1889:132. Holotype: ANSP 4635, skin, Brazil, probably Mato Grosso, São João or Chapada.
Tamandua tetradactyla nigra.—Menegaux, 1902:494. French Guiana, Cayenne, Ouanary River (MNHN 1902–62, melanistic skin).
Tamandua tetradactyla tetradactyla.—Allen, 1904, by implication; Schröder, 1937:135; Krumbiegel, 1940:175, in part; Reeve, 1942:300, in part; Cabrera, 1958:205, in part.
Tamandua tetradactyla chapadensis Allen, 1904:392; Krumbiegel, 1940: 174; Reeve, 1942:300; Cabrera, 1958:203. Holotype: AMNH 369, Brazil, Mato Grosso, Chapada.
Tamandua longicaudata longicaudata.—Beaux, 1908, by implication; Cabrera, 1958:203.
Tamandua longicaudata nigra.—Beaux, 1908:417. "Brasilien (?)."
Tamandua tetradactyla quichua Thomas, 1927:371; Reeve, 1942:300; Cabrera, 1958:205. Holotype: BMNH 27.1.1.156, Perú, San Martín, Yurac Yacu.
Tamandua tetradactyla longicaudata.—Pittier and Tate, 1932:255; Schröder, 1937:136; Krumbiegel, 1940:175; Reeve, 1942:300.
Tamandua tetradactyla kriegi Krumbiegel, 1940:171. Holotype: ZSM 1931-284, Paraguay, Estancia Zanja Moroti.
Tamandua tetradactyla straminea.—Krumbiegel, 1940:174.
? *Tamandua longicaudata mexianae.*—Cabrera, 1958:203. Type-locality: Brazil, Pará, Ilha Mexiana. Nomen nudum, not in Hagmann, 1908:29, as cited by Cabrera; no specimens from Ilha Mexiana found at PARA, MZUV, or elsewhere.

Type-locality: Brazil, Pernambuco (Thomas, 1911:133).

Range: South America east of the Andes, from Venezuela and Trinidad south to the state of Rio Grande do Sul in Brazil, the department of Cerro Largo in Uruguay (Ximénez, 1972), and the provinces of Santa Fe, Chaco, Salta, and Jujuy in Argentina.

Diagnosis: *Pelage*—color geographically variable, black vest always present only in specimens from southeastern portion of range (Fig. 1), gradating to partially vested or nonvested blond, tan or brown individuals elsewhere in range; melanistic forms from eastern foothills of Andes in Perú and Ecuador east along Amazon River to Amapá and coastal French Guiana. *Ear*—range of means of length from notch, 50–54 in all samples except 43–48 in southeastern portion of range. *Skull*—broad, with means of AOB, ORB and BW greater than 34.5, 25 and 41.5, respectively, except in samples from portions of Amazon basin and thorn forests of

northwestern Venezuela; only three orbital foramina present in at least one side of all skulls from a northwestern portion of range and in both sides of 80–100% of the skulls from eastern edge of Andes, decreasing to 60% in Amazon basin and 50% in southeastern Brazil (Fig. 3B); posterior (palatal aspect) border of infraorbital foramen an incomplete crescent, its medial border not extending as far posteriorly as its lateral border, and medial border formed either entirely by palatine or by a combination of maxilla and palatine (Fig. 3A); distance (measured perpendicular to midline of skull) between anterior borders of palatine and lacrimal bones (Fig. 3A) at least one-half distance between anterior borders of lacrimal foramen and lacrimal bone (Fig. 2); jugal relatively wide, its greatest height 31% or more of its greatest length (Fig. 3A). *Vertebral count*—25 specimens from Guyana (2, AMNH); lower Amazon basin (1, AMNH), Minas Gerais (1, MCZ), and Mato Grosso (1, USNM), Brazil; northeastern Bolivia (10, AMNH); the Chaco of Paraguay (10, CONN): cervical 7 (in 19); thoracic 17.3 (16–18, in 22); lumbar 2.5 (2–3, in 25); sacral 5 (in 25); caudal 34.5 (31–39, in 19).

Comparison: See Table 1.

Comments: Except as noted above, the extensive geographical variation within the genus prohibits a satisfactory delineation of the two species based only on external measurements and size and proportions of skulls. Both species contain large and small subspecies, clinally arranged, some undescribed and others with geographical limits incorrectly defined in the literature. The geographical span of samples compared by Reeve (1942) embraced, in the main, too wide a spectrum of subspecific variation to be useful in resolving the question of specific separation. However, my comparison of smaller geographical units, made possible by larger samples available, permits the separation of any one subspecies of *T. mexicana* from any one of *T. tetradactyla.* This is particularly striking where the geographic ranges of the two species are contiguous in northwestern Venezuela. There all measurements of body and skull, as well as pelage color and the discrete skull characters of Fig. 3, are significantly different between the two species. The features of pelage color, discrete skull characters, and certain measurements and proportions also show pronounced character displacement; examples of this displacement are shown in Fig. 4.

The isolation leading to separation into the present two species on either side of the Andes has been relatively complete as compared to events occurring in South America east of the Andes. Even so, my data indicate two centers of isolation and later dispersal there, one in the highlands of Brazil and the other in the Guyana highlands and eastern foothills of the Andes. Along the boundary between the two centers, marked roughly by the Amazon and its western tributaries, occur the greatest variation in color of pelage and a clinal decrease in size of specimens. For example, melanistic specimens have been collected from coastal French Guiana and the state of Amapá, Brazil, west through the immediate Amazon basin to the eastern foothills of Ecuador and Perú.

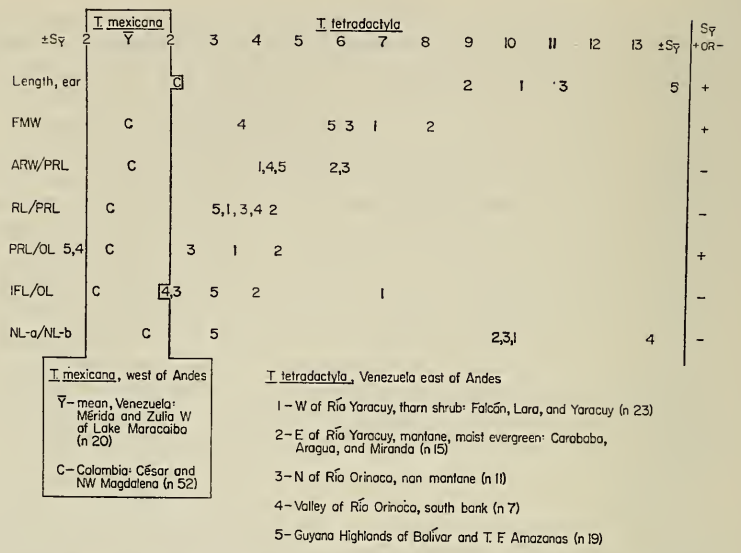

Fig. 4. Ratio diagram for measurements of *Tamandua* from juncture of the two species in northern South America. $S_{\bar{y}}$ is estimate of standard error of mean. Samples of *T. tetradactyla* are numbered 1–5 in increasing order of geographical distance from nearest population of *T. mexicana*. See text (pages 98–99) for definitions of abbreviations used for cranial measurements.

This distribution coincides with the areas of major variation between nonvested and vested forms. The inclusion of a figure entitled "Le Tamandua noir, variété du Tamandua ordinaire" in Azara (1809:plate 7) must be disregarded as evidence that melanistic tamanduas have been found in Paraguay. Azara (1801 and 1809) made no textual reference to melanistic tamanduas. The plate in question is a composite of a giant anteater, *Myrmecophaga tridactyla* L., and a black *Tamandua tetradactyla* (L.). The lateral head stripe and contours of the head, ears, and apparently the 1st and 2nd claws (despite depicting digits 1, 2 and 4 as medial to the longest claw on digit 3) are those of *Myrmecophaga tridactyla*, while the remaining body, legs, and tail are those of *Tamandua*. The textual description (Azara, 1809:255) cited for this plate is for *M. tridactyla*. Desmarest (1817:107) referred this figure to the black tamandua, *M. nigra* (presumedly that of Geoffroy St.-Hilaire, 1803:217, which in turn is based upon MNHN 431 from "La Guyane?") without reference to geographical origin. I have found no melanistic specimens from Paraguay, Mato Grosso or Bolivia, an area containing both vested tamanduas and those having only black shoulder stripes.

The melanistic tamanduas are, perhaps, examples of the saturate stage before progressive subtraction of melanin to paler, more uniformly colored indivuals as discussed by Hershkovitz (1968). This may have been triggered by cross-mating between populations formerly isolated in late Pleistocene along the Andean foothills and the Guyana highlands with those from the highlands of Brazil (see Vanzolini, 1973). An alternate explanation of the distribution of melanistic forms could begin with a population having a high incidence of melanism that spread from the foothills of the Andes easterly along the Amazon drainage to the Atlantic coast. This does not explain the evidence of clinal variation in size, the highly variable pelage, and differences in orbital foramina as does the concept of two dispersal centers.

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